

The enclosing latticed sphere of *Tuscaridium cygneum* (Murray), a eurybathyal phaeodarian Radiolaria, from the North Pacific

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Abstract. Specimens of *Tuscaridium cygneum* (Murray), the eurybathyal phaeodarian Radiolaria, from the eastern temperate North Pacific Ocean were enclosed in an intricate latticed sphere in *in situ* samples. Scanning electron microscopy revealed unique microstructures on the shells of individual radiolarians and on the spheres. Although the function and significance of the enclosing spheres are unknown, colonies of these deep-dwelling, bioluminescent phaeodarians may be common in the world's oceans.

Key words: Enclosing latticed sphere, eurybathyal phaeodarian, North Pacific, Radiolaria, *Tuscaridium cygneum*

Introduction

The occurrence of phaeodarian radiolarians in the depths of the ocean has been well documented since 1885 (Murray, 1885; Haeckel, 1887; Haecker, 1904, 1908; Reshetnyak, 1966; Takahashi, 1987). Furthermore an association of phaeodarians with latticed spheres has been known since the beginning of this century. Haecker (1904, fig. 17 as *Tuscarusa chuni*; 1908, figs. 222, 223) illustrated some individuals of *Tuscareta globosa chuni* (Borgert) from the "Antarctic drift" which were attached to the surface of a "shell". He suggested that they were in colonies and that each individual hung to a "shell" of double-layered lattice network. Takahashi's photograph of *Tuscaridium cygneum* from the subarctic Pacific (1987, fig. 11g) shows that some of the 16 individuals associated with a sphere appear to attach to the sphere with their oral end, probably with their long oral spines. Here we report specimens of *Tuscaridium cygneum* which were completely enclosed in a latticed sphere collected off California.

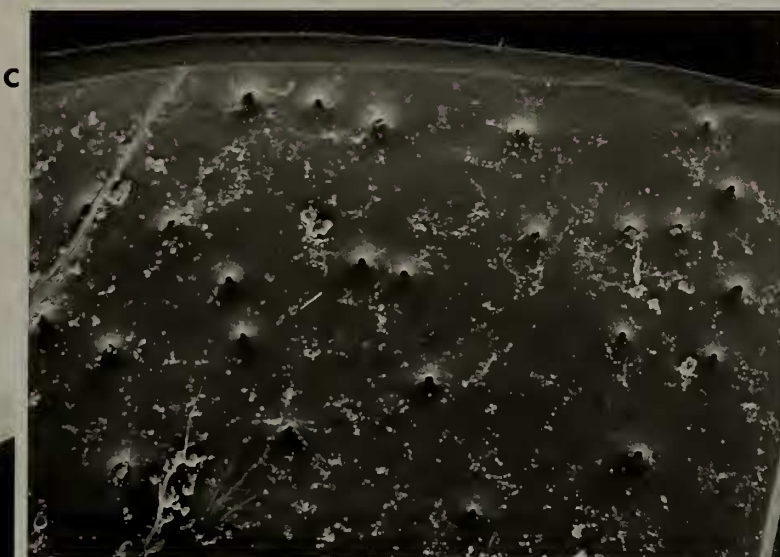
Collection

Specimens were collected on cruises with Dr. James J. Childress, University of California, Santa Barbara, using an opening-closing 10-m² Tucker-trawl with a 30-liter thermally insulated closing cod end (Childress *et al.*, 1978). Ship speed was kept below 1 knot during the horizontal tows to minimize damage to specimens caused by the net. This system is effective in recovering fragile deep-sea organisms (e.g. Thuesen and Childress, 1994). Specimens examined in this study were collected in a 2,600 m deep trawl, approximately 160 km west of Point Conception, California (35°01'N, 122°50'W) in March, 1993. Additional specimens were obtained from a depth of approximately 900 m near the same location (34°55'N, 122°57'W). The specimens were always found to be colonial in nature and appeared to be alive when recovered, since upon mechanical stimulation in a shipboard darkroom they produced a blue bioluminescent glow characteristic of photoprotein-bearing radiolarians (Campbell and Herring, 1990; unpublished data). The specimens used for SEM were fixed in approximately 4% formalin. The radiolarians are identified as *Tuscaridium cygneum* (Murray).

Figure 1. Microstructure of *Tuscaridium cygneum* (Murray). **A.** A specimen with four incomplete radial tubes at the oral end and a caudal spine. Oral spines are broken off during the preparation. Scale bar=556 μ m. **B.** Outer shell wall with irregularly scattered holes which are the outer ends of the canals. Scale bar=50 μ m. **C.** Solid shell wall (top) and irregularly scattered holes which are the inner ends of the canals. Note elevated areas surrounding the holes. Scale bar=50 μ m. **D.** Details of the shell wall (top) showing the solid, porcellaneous and opaque nature of the wall and irregularly scattered holes which are the inner ends of canals. Note elevated areas surrounding the holes. Scale bar=26 μ m. **E.** Distal end of the shell and a caudal spine. Note lineate surface structure and scattered bristles on the surface. Two pedal pores are visible at the proximal end of the spine. Scale bar=67 μ m.



A



C



D



E

Taxonomy

Family Tuscaroridae Haeckel, 1887

Original description.—"Phaeodaria with an ovate, spindle-shaped, or nearly spherical shell exhibiting a peculiar solid porcellaneous structure; with a few radial pores around the base of the hollow tubules, which are symmetrically arranged around the main axis and the mouth. Surface of the shell smooth or spiny, not tabulate nor panelled".

Remarks.—Haeckel (1887, p. 1703) further discussed "... a solid porcellaneous shell, which is perfectly opaque, milky-white or yellowish-white when dried and has a smooth surface (not tabulated or panelled). The shell wall is solid, but is pierced by innumerable very fine pores, which everywhere pierce the thick, apparently solid, fundamental substance of the shell wall".

Genus *Tuscardium* Haeckel, 1887

Haeckel, 1887, p. 1709; Borgert, 1905, p. 108; Haecker, 1908, p. 225.

Type species.—*T. cygneum* (Murray, 1885).

Original description.—"Tuscarorida without radial aboral feet, but with a terminal axial caudal foot, and a variable number of circoral teeth".

Remarks.—Among the three genera of the Family Tuscaroridae, the genus *Tuscardium* is characterized by its spindle-shaped (vs. ovate or subspherical) outline, its possession of an aboral (=terminal, axial, or caudal) spine (=foot), but the absence of radial aboral feet. (The genus *Tuscarora* bears three equidistant aboral radial feet, while *Tuscarusa* has four equidistant aboral radial feet.) In addition, *Tuscardium* also

possesses four radial tubes, dorsal and ventral pairs, at the oral end, which extend nearly horizontally. The mouth is prolonged into a cylindrical, spinulate proboscis which curves towards the ventral face of the shell (Haeckel, 1887).

Tuscardium cygneum (Murray, 1885)

Figures 1, 2

Tuscarora cygnea Murray, 1885, p. 226, pl. A, fig. 20.

Tuscardium cygneum (Murray) Haeckel, 1887, p. 1709-1710.

Tuscardium lithornithium Haeckel, 1887, p. 1710, pl. 100, figs. 8, 8a.

Tuscardium cygneum (Murray) Haecker, 1908, p. 226, pl. 26, fig. 204, pl. 32, fig. 243, pl. 33, fig. 254; Reshetnyak, 1955, p. 98; 1966, p. 163, pl. 1, fig. 3.

Original description.—"Shell spindle-shaped, twice as long as broad (in the transverse section circular) equally tapering towards both poles of the main axis. The aboral pole bears a thin, cylindrical, straight, caudal spine, placed in the prolongation of the main axis, and about half as long as the shell. Its base is pierced by two large opposite pedal pores. The anterior or oral pole bears a cylindrical peristome, similar to a bird's head, and curved towards the ventral face; on both sides of its neck (at right and left) a series of three or four irregular, ovate, buccal holes. The neck bears four cylindrical, spinulate, radial tubes (two on each side), crossed nearly horizontally, and placed in two diagonal planes perpendicular one to another; these planes correspond to those in which four feet of *Tuscarusa* medusa lie. The base of each tube is pierced by four dental pores".

Remarks.—Haeckel (1887) reported two species within the genus from his *Challenger* samples in the tropical Central North Pacific: *T. cygneum* from Station 250 and *T. lithor-*

Table 1. The occurrence and measurements of *Tuscardium cygneum* (Murray).

Location	Depth (in m)	Length (in mm)	Width (in mm)	Investigator
central North Pacific	5,490	3.6	1.8	Haeckel (1887)
	5,582	3.2	1.6	Haeckel (1887)
equatorial South Atlantic	3,500	2.9-3.0		Heacker (1908)
Northwestern Pacific	50-200, 200-1,000,			Reshetnyak (1966)
	1,000-2,000, 4,000-8,000			
Okhotsk	3,395	1.43-1.46 (av. 1.44)		Reshetnyak (1966)
Indian Ocean	1,500			Reshetnyak (1966)
eastern Subarctic Pacific	4,200			Takahashi (1987)
off California	900, 2,600	2.70-2.79 (av. 2.74)	1.30-1.37 (av. 1.34)	this paper

Figure 2. Microstructure of *Tuscardium cygneum* (Murray). **A.** Right ventral view of the cephalis and cylindrical radial tubes with scattered bristles. Scale bar=333 μ m. **B.** Details of the oral part and bristly proboscis of the same specimen. Note that all the bristles are located on the top of a slight conical elevation thus appearing as an irregular surface. Also the distal end of the proboscis terminates in irregular scalloped edges and with some needle-like projections. Scale bar=111 μ m. **C.** Dorsal left view of the oral part with helmet-like proboscis. Note that the proximal part of radial spines possesses a lineation and bristles on the surface. Scale bar=111 μ m. **D.** A colony of eight specimens and the enclosing lattice sphere. Diameter of the sphere is 12.6 mm. **E.** Details of a single-layered geodesic latticed sphere. Note the short spines projecting outward from slightly elevated nodal points and the web among the silica rods. Scale bar=100 μ m.



A



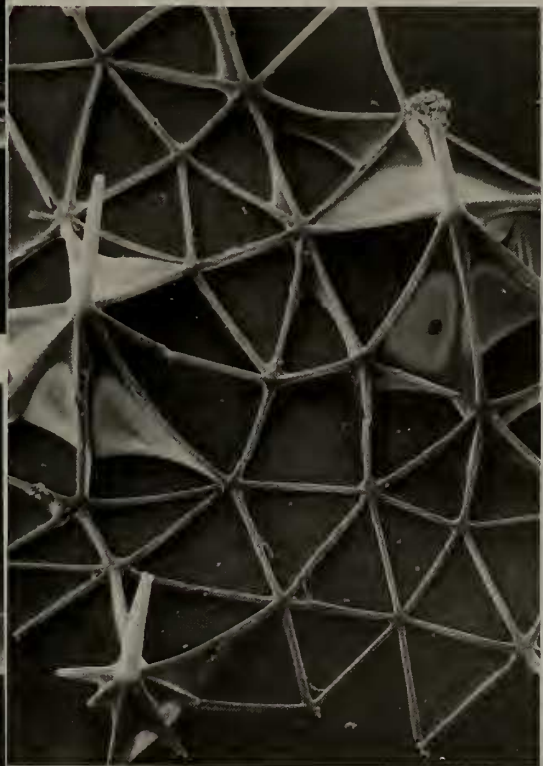
D



B



C



E

nithium from Station 264. Although their overall lengths are similar, *T. cygneum* and *T. lithornithium* differ in (a) the number of dental pores (4 vs. 6–8), (b) the number of pedal pores (2 vs. 4), and (c) the surface of the aboral and apical spines (smooth vs. spiny).

Haecker (1908) noted similarities between specimens he collected from the equatorial South Atlantic and *T. cygneum* described by Haeckel from the Pacific, especially in the exceptionally bristle nature of the peristome and the spine. Despite the small length of his Atlantic specimens as compared to those from the Pacific (2.9–3.0 mm vs. 3.2–3.6 mm), Haecker concluded that all the specimens should be considered conspecific.

Apparently the species has considerable length variations because in the Okhotsk Sea (Reshetnyak, 1966), it ranges from 1.43 to 1.46 mm (average 1.44 mm), while our California specimens range from 2.70 to 2.79 mm (average 2.74 mm; N=5) (Table 1). It also has a wide geographic distribution and is found at a variety of depths (Table 1).

Discussion

Microstructure

In our discussion below, we generally follow the terminology of Haeckel (1887) and Haecker (1908) except for the enclosing sphere (see below). New features recognized based on the present investigation are italicized hereafter. According to Haecker (1908), in the living organism the cephalis is located below while a long single caudal spine points upward. However, in the colony, individuals are apparently randomly oriented within the sphere.

Shells.—The shell is oval to pear-shaped in outline (Figure 1-A). Numerous holes are scattered irregularly all over the surface (Figure 1-B) of the porcellaneous and opaque shell wall (Figures 1-C, D). These are actually the outer ends of the canals which pierce through the solid wall and end as smaller holes on the inner wall with slight inward protrusions (Figures 1-C, D).

The cephalis is covered by an irregular surface with bristles at its top (Figures 2-A–C), which both Haeckel (1887) and Haecker (1908) described as "spiny". A helmet-like proboscis covers the mouth and its distal end terminates in irregular scalloped edges with needle-like projections at each cusp (Figures 2-B, C). Four long cylindrical radial tubes, the oral spines, are divided into right and left pairs. Numerous holes of different sizes are observed both on the peristome (buccal holes of Haeckel) and the proximal part (dental pores of Haeckel) of the tubes (Figures 2-B, C). The very end of the proximal part of the tubes shows lineate ridges but becomes smooth distally, and bristles are scattered along the surface of the tube.

At the aboral end of the specimen, the shell tapers into a long caudal spine with many distinct linear ridges (Figure 1-E) which extend all the way to the distal end. Four oval-shaped pedal pores (Figure 1-E) are located at its proximal end. The surface of the caudal spine is also covered with bristles, but compared to Haeckel's (1887, pl.100, fig.8) specimen from the Pacific, they are few in number.

The enclosing sphere.—The interest of the present study, aside from the unusually large size, unique shell structure and morphology, is that all of our specimens are found not individually but are completely enclosed in a latticed sphere (Figure 2-D). This is not only the first such report for the present genus in the California Current, but also the first time we have encountered this throughout our investigations of plankton samples.

For the enclosing sphere, we use the term "latticed sphere" instead of "latticed shell" (= Gitterschale, German of Haecker and Borgert) in order to differentiate the shell (= Schale, German) of an individual Radiolaria. The complete enclosing sphere measures 12.6 mm in diameter. It consists of a single-layered, geodesic-like sphere, formed by cylindrical rods, 0.1 mm in length, which connect into triangles of different sizes. Qualitative spot mode analysis with an energy-dispersing spectrometer indicates that the rods are made of silica, as expected. Short cylindrical spikes project outward from several elevated nodal points where silica membranes form a web among the rods (Figure 2-E).

Although shells of our California specimens are completely enclosed within a single-layered latticed sphere, some shells of this species from the eastern Subarctic Pacific (Takahashi, 1987) are located outside of the sphere with their oral ends toward the sphere.

Such an orientation of the oral end toward or penetrating inside the sphere, while the major part of the shell remains outside, has been observed in other phaeodarians. Haecker (1904, 1908) reported that all the shells of *Tuscaretta globosa* (Borgert) were outside of a double-layered latticed sphere. They attached by sticking both oral spines and the proximal part of their four strongly recurved aboral spines into the sphere (1904, fig. 17; 1908, figs. 222, 223) as is the case with *T. passeracula* Haecker (1908, fig. 181).

The shells of our specimens are held in position within the sphere by their long spines. The sphere, although fragile, does not collapse if held out of the water (Takahashi, 1987). Because we do not know whether the sphere is filled with sea water or some other fluid, its contribution to the buoyancy of a colony has not been determined.

The mechanism by which the sphere is formed is also not known. Because radiolarians cannot get inside once the sphere has been made, either individuals of a colony are reproduced inside the sphere after its formation (for example, through fission), or the sphere is formed collectively by a group of individuals. The spherical shape of the latticed sphere appears incongruous with the asymmetry of the radiolarians themselves but its formation is probably affected by external physical constraints, just as pressure and surface tension determine the shape of a bubble.

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